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The six hundred and fortieth meeting of the Club was held at the Rubens Hotel, London, on the 17th January, 1967.

Chairman: Mr. R. S. R. Fitter

Members present: 22; Guests 6.

Mr. Martin Woodcock spoke on birds seen by him in parts of Thailand and Malaya, illustrating his talk with coloured slides.

Secondary intergradation amongst bulbuls of the genus *Pycnonotus* in the Transvaal Province, South Africa

by MILES B. MARKUS
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Bulbuls of the genus *Pycnonotus* Boie are found throughout the Republic of South Africa where the vegetation is suited to their requirements. The various forms are currently treated by certain authors as races of a single species whilst other specialists recognise three distinct species. Purely for convenience in the discussion below the latter, perhaps more conventional, view is taken. The three closely related groups, *Pycnonotus capensis* (Linnaeus) 1766, *P. barbatus* (Desfontaines) 1787 and *P. nigricans* (Vieillot) 1818 occupy basically discrete geographical areas, overlaps of their respective ranges being comparatively limited in extent.

They are not restricted to such dense vegetation as the other South African Pycnonotidae, though on the whole *capensis* and *barbatus* occur in thicker bush than *nigricans* which, over most of its range, is an inhabitant of more open country. They all appear, as regards the drab nature of their plumage, to be adapted for life in reasonably open vegetation. Brooke (1965) attaches reversional significance to an abnormal yellowish wash on the throat of an albino *barbatus* in the National Museum, Bulawayo, suggesting that this may be an indication that the genus *Pycnonotus* as a whole represents a successful attempt by a group of forest birds to invade the savannas and that during the course of this expansion "yellow pigments have become scarcer in the plumage thus producing the dark brownish bulbuls out of green forest birds". In this regard it may be noted that in the Transvaal Museum at Pretoria there is a partially

albinistic example (a flat skin) of nigricans from Keimoes in the northern Cape Province that is yellowish interramally. Capensis, barbatus and nigricans have, near the joint between the antebrachium and manus, yellow markings, clearly visible on white feathers which are situated mainly on the under surface of the wing. These might also be considered as possible evidence of a recent change of habitat. The colouring is, on the average, clearer in capensis and barbatus than in nigricans from more arid areas. Better known is the fact that all the South African Pycnonotus forms have yellow under the tail and that some of the races from less arid

areas can have olive markings on the upper parts.

For the three major bulbul groups to have developed their present individuality, the gene flow in an ancestral pycnonotid population inhabiting South Africa must on at least one occasion in the geologic past have been disrupted. From a perusal of the literature it becomes increasingly obvious that our knowledge of what happens in the areas where one of the three resultant segregates gives way to another is insufficient for a proper evaluation and appreciation of the amount of evolutionary divergence that has taken place between them as a result of past differentiation in the geographic species fission process. If taxonomists are to reach greater agreement than at present in regard to their treatment of the nomenclatorial problem presented by these birds, it is imperative that the situation in such transition zones be investigated in considerably greater detail than has been done up to now.

A series of 10 adult specimens (see below for details) in worn plumage which bridge the morphological gaps between *barbatus* and *nigricans* has recently been collected (by A. N. Markus and the author) approximately 5 miles north of Fochville in the Transvaal. All were shot in the same mulberry tree, two on 2 October 1965 and eight on 21 October 1965. They are now housed in the South African Museum, Cape Town. Each bird is referred to below by its respective South African Museum (S.A.M.)

registration number.

METHODS

Specimens were weighed in grammes immediately after collection. After weighing, a longitudinal incision was made in the centre of the abdomen and the proventriculus, gizzard, intestine and part of the liver dissected out together with associated tissues. Ovarian condition and testicular dimensions were recorded and the testes placed in Bouin's fixative for subsequent laboratory determination of the stages of spermatogenesis. The microtomized sections, cut at 5μ , were stained with iron haematoxylin to reveal nuclear details. Orange G was used as a counterstain.

It is not possible to determine accurately the original nature of the eyelid/ eye-wattle of a hybrid from a skin as desiccation soon causes a reduction in the size of these structures; this is accompanied by a *post mortem* colour change. The skin surrounding the eyes was therefore examined in the field and details noted. The partially eviscerated cadavers

were refrigerated and skinned later.

Weights and measurements for the wing (flattened), tail, bill and tarsus are given in Tables I (33) and II ($\mathbb{Q}\mathbb{Q}$). S.A.M. 55255 e was damaged by shot and could not be sexed. The "bill" was measured from the anterior margin of the nostril to the tip of the upper mandible; and the "tarsus"

at the back, from the point of the joint between the tibia and metatarsus to the basal joint of the hind toe (distally). The wing and tail measurements represent minimum lengths as the tips of the longest remiges and/or rectrices of many of the specimens were abraded. Measurements are in millimetres. In view of the heterogeneous nature of the sample, means have not been calculated as they would have no significance. Weights are not available for all the bulbuls. Qualitative and other information is given below for each individual separately. In every case the irides were red (the irides of nigricans are typically red; those of barbatus are usually brown, though sometimes reddish).

NOTES ON INDIVIDUAL SPECIMENS

S.A.M. 55255 a

\$\oint\$, 2 October. Not in breeding condition. More like *nigricans* on the throat than *barbatus*. Eye-wattle poorly developed and dark brownish-black externally though yellower on the bottom lid towards the temporal canthus. Inner surfaces of both lids bright orange near the outside instead of the normal yellow, this being less marked on the lower lid.

S.A.M. 55255 b

\$\, 2 October. Ovary slightly granular, largest oocyte 1 mm. in diameter. On throat more like *barbatus* than *nigricans*. Eye-wattle similar to that found in normal *nigricans*; colour orange.

S.A.M. 55255 c (mate of 55255 d)

 \circlearrowleft , 21 October. Left testis 9.0 x 6.0, right 9.0 x 6.25; the height of spermatogenetic activity had been reached and bunched sperms are present in all the seminiferous tubules. Similar in plumage to P. n. superior Clancey, 1959. Eyelids larger than in typical barbatus but not as well developed as in typical nigricans. In colour a mixture of yellowish-khaki and dark greyish-black, less of the latter in the region of the temporal canthus. The inner lining was yellow (normal).

S.A.M. 55255 d (mate of 55255 c)

\$\,21\$ October. Not in breeding condition. Throat coloration intermediate between *barbatus* and *nigricans*. Wattle similar to that of *nigricans*; yellowish-orange, becoming yellow on the inside.

S.A.M. 55255 e

Collected on 21 October. The gonads of this specimen were shot away together with most of the back where the oviducts in the \mathcal{D} or vasa deferentia in the \mathcal{D} are normally situated, so the sex could not be determined. The throat is not like that of *nigricans* and approaches the condition in *barbatus*. Eyelid black externally, indistinguishable from that of *barbatus*. Colour of inner lining also normal. Bill 10 mm., wing 99 mm.

S.A.M. 55255 f (mate of 55255 g)

3, 21 October. Left testis 10.75 x 6.5, right 10.0 x 7.0; full spermatogenesis has occurred and discharge of spermatozoa through the tubule lumina has begun. In plumage similar to *P. n. superior*. Eye-wattles well developed. On the upper lid mainly dark greyish-brown, the inner lining an unusually bright yellow; dark greyish-brown mixed with yellowish-khaki on the lower lid, the colour of the lining being yellowish-khaki.

TABLE I MEASUREMENTS AND WEIGHTS (ನೆನೆ)*

No. of specimen	Wing	Tail	Bill	Tarsus	Weight
S.A.M. 55255 c S.A.M. 55255 f S.A.M. 55255 h S.A.M. 55255 i	102·5 103·0 98·0 101·0	94·0 92·0 86·0 90·5	11·0 11·75 11·0 12·0	23·0 23·0 22·0 22·0	38·5 39·0 38·5 38·0
Range	98–103	86–94	11–12	22–23	38-39

^{*}Lawson (1962) gives, inter alia, the following measurements for Pycnonotus barbatus layardi Gurney (14 \circlearrowleft): wing 96·0–106·5 (av. 99·6), tail 85·0–99·0 (av. 88·8); and for P. nigricans superior Clancey (16 \circlearrowleft): wing 97·0–108·0 (av. 99·8), tail 84·0–95·0 (av. 87·7).

TABLE II MEASUREMENTS AND WEIGHTS (♀♀)*

No. of specimen	Wing	Tail	Bill	Tarsus	Weight
S.A.M. 55255 a	97.0	87.0	10.5	22.0	
S.A.M. 55255 b	97.5	86.0	11.0	22.0	
S.A.M. 55255 d	92.0	-	10.0	22.0	33 -0
S.A.M. 55255 g	98 · 0	86.0	11.0	22 · 5	37.0
S.A.M. 55255 j	100.0	90.0	11.0	21.0	34 · 5
Range	92–100	86–90	10-11	21-22 · 5	33–37

^{*}Lawson (1962) gives, *inter alia*, the following measurements for *Pycno-notus barbatus layardi* Gurney (15 $\varsigma\varsigma$): wing 92·0–96·5 (av. 94·3), tail 80·0–97·5 (av. 84·5); and for *P. nigricans superior* Clancey (16 $\varsigma\varsigma$): wing 92·5–101·5 (av. 96·3), tail 80·0–88·0 (av. 83·4).

S.A.M. 55255 g (mate of 55255 f)

2, 21 October. Largest oocyte 1 mm. in diameter. Throat intermediate between *barbatus* and *nigricans*. Wattles well developed and mainly dark greenish-grey, becoming light orange towards the inside and towards the temporal canthus. Inner lining yellow (normal).

S.A.M. 55255 h

3, 21 October. Left testis 5.25×3.5 , right 3.5×2.5 ; tubules enlarging, containing secondary spermatocytes and spermatids. Some spermateleosis has taken place. Throat similar to *nigricans* but not as wholly black as in typical *nigricans*, in this respect tending towards *barbatus*. Wattle well developed, orange.

S.A.M. 55255 i

3, 21 October. Both testes measure 9.75×6.5 ; bunched spermatozoa have been formed in the seminiferous tubules. Many sperms are free in the lumina. Plumage as in *P. n. superior*. Wattle well developed, orange.

S.A.M. 55255 j

\$\oint\$, 21 October. Largest oocyte 1 mm. in diameter. Indistinguishable from \$P. n. superior\$ as regards plumage. Wattle well developed, orange.

DISCUSSION

Because of the fact that the plumage characters of nigricans and of the austral races of barbatus are so very similar, it is not always easy to recognise an intermediate specimen and this may be one of the reasons why relatively few of these are known. Barbatus, however, does not have the full black chin which is characteristic of nigricans and this is the most constant and obvious distinction between the two; and whereas nigricans normally has a well developed orange to reddish-orange wattle surrounding the eye, the eyelid in typical barbatus is black externally. One of the Fochville birds when collected had a black eyelid, indistinguishable from that of barbatus, five had an orange wattle as in nigricans and four were variably intermediate, a phenomenon resulting from recombination of the parental genomes. Varying degrees of intermediacy as regards the throat colour are also evident. Similar variation about the throat has been noted amongst apparent hybrids from other localities e.g. by Winterbottom (1966) for birds from the Okavango. Random interbreeding at Fochville of hybrid progeny with individuals of the same and other filial generations and with the parental types probably occurs, this accompanied by Mendelian assortment and segregation. There are probably few direct F4 hybrids in this variable intermediate subpopulation which is basically composed of bulbuls differing from each other and from the more homozygous parental norms, barbatus and nigricans, by a few of the many hereditary units by which these two populations differ. The expression of any genotypic heterozygosity in S.A.M. 55255 i and S.A.M. 55255 i. which are not visibly separable from typical nigricans, is likely to be obscured by one or more such possible complicating factors as gene interaction, some genes interfering with the action of others, dominantrecessive allelic control and the presence of fewer or more polygenes; the latter have a cumulative action and incomplete or no dominance. Evidence of hybridization can thus be masked.

That unlike phenotypes will mate is shown by the irregular sexual dimorphism of one of the two "identified" pairs of birds that were taken. On the basis of their behaviour these were assumed to be paired. The two pairs are S.A.M. 55255 c and 55255 d; and S.A.M. 55255 f and 55255 g. It will be noted that gametogenetic activity in the females has lagged behind that in the males but this is normal. Markus (1963 a) refers to a third pair from the South-western Transvaal. The eye-wattles were "rather a light brownish-khaki, becoming yellowish towards the inside, thus intermediate in coloration between P. b. layardi and P. nigricans . . ." Those of one bird were slightly darker than those of the other, the plumage

of both resembling that of P. b. layardi Gurney, 1879.

Additional instances of the occurrence of unusual eyelids/ eye-wattles are provided by White (1956) (Angola) and Markus (1963 b) (Transvaal). Mr. O. P. M. Prozesky has drawn my attention to fresh specimens in the Transvaal Museum that are also intermediate in this regard (from Tuli Block on the eastern border of Bechuanaland). Irwin (1958) records a pair of birds with dissimilar but normal wattles (Bechuanaland).

It should be borne in mind that natural selection is probably not operating against bird hybrids if they are as numerous in the hybridization belt as are the parental types in their respective areas, if hybrid sterility and lack of viability are not apparent and if there is a minimum of evidence of preferential mating between like phenotypes. Where this is so, "regardless of the morphological differences between the parental populations, they must be treated as conspecific for so they have proved themselves' (Sibley, 1959).

In normal P. b. lavardi the inner surfaces of the evelids, notably the upper lids, are lined with yellow near the outside although the external surfaces themselves are black (Markus, 1965). Mr. Peter Woodall (pers. comm.) recently informed me that the yellow pigmentation was also present in a Salisbury bird that he checked. Bulbuls in the latter area have. quite correctly in my opinion, been separated from P. b. layardi by Lawson (1962) as P. b. naumanni Meise (P. c. naumanni) and it seems probable that the yellow lining to the eyelids will be found in the other forms of barbatus as well. It is interesting to note that certain of the Fochville birds, apart from the intermediate appearance of their eye-wattles externally, were also anomalous as regards the colour of the inner pigmentation and this fact would seem to lend support to an earlier suggestion (Markus. 1965) that the presence of the normal yellow lining in P. b. layardi is a heritable trait linking barbatus (eyelid black externally) with nigricans

(eve-wattle orange externally).

The histological results (see above) demonstrate conclusively that the testes of males which are morphologically intermediate between barbatus and nigricans can produce gametes but prove nothing beyond this e.g. determination of gametic viability is not possible. Any genetic incompatibility between the two groups has not been of such a nature as seriously to affect the normal spermatogenetic process. It remains to be ascertained whether or not barbatus x nigricans heterozygotes are completely balanced physiologically, both somatically and with regard to the germinal tissues; also whether effectively interbreeding bulbul populations in such contact hybridization zones have reduced viability or whether they are heterotic in any way. It is not yet known if there is any sexual difference in the degree of hybrid fertility or if there is any perceptible chromosomal divergence between barbatus and nigricans, either structurally or numeri-

The replacement zone in the Transvaal in which hybrids are found is not extensive, for intermediates are not normally found at any great distance from it. Markus (1963 b), however, records the case of a bulbul indistinguishable from P. b. layardi as regards plumage but with the skin around the eye lemon-yellow instead of black. The locality in which it was trapped lies within and not on the periphery of the range of P. b. layardi and it was suggested that the bird might be a mutant or that the yellow eye-wattle represented an ancestral condition and was an atavism due to gene interaction. Dr. R. M. Harwin (pers. comm.) has remarked that this individual could be the offspring of a dry season nigricans wanderer which moved out if its normal range and then stayed behind and interbred with P. b. lavardi. This is also a possibility. The two forms are certainly very similar with regard to voice and behaviour but to date no detailed analyses have been undertaken.

CONCLUSION

Barbatus and nigricans seem not to be mature species, evolutionarily speaking, even though they may appear to be fully distinct species phenotypically.

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A new subspecies of the Wattled Bulbul Pycnonotus urostictus. of the Philippines

by Kenneth C. Parkes

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The endemic Philippine bulbul Pycnonotus urostictus is currently divided into three subspecies, characterized by Delacour and Mayr (Birds of the Philippines, 1946: 174) as "rather indistinct." Rand and Rabor (Fieldiana: Zoology, 35, 1960: 428), whose material was admittedly inadequate, provisionally accepted the three named races, stating that the differences observable in their series were "about at the level used to characterize lightly marked subspecies". On the basis of the characters presently used to define the three subspecies, namely the amount of white on the abdomen and the shade of colour of the brown upperparts, these authors are justified in considering the races recognizable but not strikingly